Geographic variation in sexual dichromatism in birds

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The tendency for insular bird populations to "lose" bright male plumages, leaving males dull-plumaged and similar to females, is well documented (Bateson 1913, Mayr 1942, Lack 1947), with examples occurring on nearly every major island group supporting an endemic avifauna. This phenomenon has been explained chiefly by one mechanism:

> The loss of sexual dimorphism through feminization of the male plumage seems to develop only in well-isolated and rather small populations . . . It . . . seems to occur only in localities where no other similar species exist, i.e., where a highly specific male plumage is not needed as a biological isolating mechanism between two similar species.
>
> Ernst Mayr (1942)

Later authors have for the most part followed Mayr's lead (e.g. Lack 1947, Sibley 1957, Grant 1965), although some additional explanations (discussed below) have been advanced for specific cases.

A brief review of examples of this phenomenon led me to see that Mayr's explanation does not adequately account for the diversity of situations in which geographic variation in sexual dichromatism occurs. The purpose of this paper, therefore, is to review geographic variation in sexual dichromatism in birds, and to develop potential explanatory hypotheses.

Methods

Examples of geographic variation in sexual dichromatism were assembled from a variety of sources: published accounts including taxonomic treatments, regional works [especially the atlases of speciation in Africa of Hall & Moreau (1970) and Snow (1978)], and the many reports on the results of the Whitney South Sea Expeditions and the Archbold Expeditions; examination of specimens in the Field Museum of Natural History, American Museum of Natural History, U.S. National Museum of Natural History, University of Michigan Museum of Zoology, Louisiana State University Museum of Natural Science, and University of Kansas Natural History Museum; and consultation with knowledgeable ornithologists. The list presented herein is certainly incomplete—my hope is simply that it is a sufficiently large and representative sample that insights into the phenomenon will be possible.

To preserve clarity of patterns, I limited the examples analysed in the present paper to those occurring within biological superspecies (Mayr 1963). Decisions as to what constitutes a superspecies were often somewhat arbitrary; however, borderline cases were excluded. Species exhibiting variation in coloration of one sex *not* in the direction of the coloration of the other sex, including many examples of heterogynism (Hellmayr 1929, Mayr 1963), were excluded because no variation existed in the degree of dichromatism. Examples in which geographic variation in age of attainment of adult plumages caused variation in sexual dichromatism were included only when the variation was extreme, and not simply variation in the proportion of males in subadult plumages.

When possible, the direction of change and the minimum number of evolutionary derivations were inferred based on outgroup comparisons and geographic considerations. If all other members of the species group or genus showed one general pattern of sexual dichromatism and the same pattern was found in some but not all populations of the species of interest, then that pattern was assumed to represent the primitive state. If different populations gained or lost bright coloration on different parts of the body, or if populations showing variation in dichromatism were geographically separated by populations showing the primitive state, then each population was counted as an independent evolutionary derivation.

A set of abbreviations was employed to summarize patterns of variation. Males are listed first, then females. "B" and "D" refer to "bright-plumaged" and "dull-plumaged", respectively, and "+" indicates "brighter-plumaged than". For example, a population with bright males and dull females is B/D; a population with brighter-plumaged females relative to the first is B/D+; one with females identical to bright-plumaged males is B/B; and so on. Descriptions of populations as bright- or dull-plumaged are relative—a "bright" swift is much duller than a "dull" trogon. Also, the abbreviation for a population's dichromatism is dependent on the type of dichromatism found in the remainder of the populations of that superspecies—a sexually monochromatic species with one population in which males are brighter would be D/D; however, a sexually monochromatic species with one population in which females are duller would be B/B.

Results

Examples of geographic variation in sexual dichromatism in 158 species of birds representing 43 families are summarized in the Appendix. Within particular species, multiple derivations of variant populations were common. Several patterns were present: between-population variation was discrete (stepped) in some examples (e.g. *Foudia rubra*, *Petroica multicolor*), and clinal in others (e.g. *Ficedula hypoleuca*, *Molothrus aeneus*, *Dendroica pinus*). Within-population variation was continuous in some species (e.g. *Pyrocephalus rubinus*), and polymorphic in others (e.g. *Terpsiphone mutata*). Both types of within-population variation occurred in different populations of Tourmaline Sunangels *Heliangelus exortis* (Bleiweiss 1985a).

Of the 158 instances of geographic variation in sexual dichromatism, at least 107 involved changes in male plumage brightness (left half of

TABLE 1
Geographic situation and directionality of change in plumage brightness for each sex, based on examples of geographic variation in sexual dichromatism in the Appendix for which directionality could be determined

Geographic situation	Male		Female	
	B→D	D→B	B→D	D→B
Insular	29	7	3	11
Allopatric	12	1	1	1
Allopatric–parapatric	2	0	0	8
Parapatric	4	2	1	5
Parapatric–clinal	1	0	0	2

table in the Appendix), whereas at least 90 examples were of changes in female plumage brightness (right half of table). Hence, variation in the coloration of either sex was about equally likely. However, in species for which the direction of change could be determined, the direction (i.e. bright to dull, dull to bright) was decidedly nonrandom (Table 1). Males were nearly five times more likely to lose bright plumage than to gain it (compared with uniform distribution, $\chi^2=24.9$, df=1, $P<0.05$); females were more than five times more likely to gain bright plumage than to lose it ($\chi^2=15.1$, df=1, $P<0.05$). This significant interaction between sex and directionality of change of coloration ($\chi^2=38.2$, df=1, $P<0.05$) clearly reflected the fact that males of most species are bright-plumaged to begin with, and that females of most species are initially dull-plumaged.

The geographic situation of examples of variation in levels of sexual dichromatism had little bearing on the directionality of change. Although males of island populations were more likely to lose than to gain bright coloration (Table 1), no significant interaction between geographic situation (insular vs. continental) and gain vs. loss of bright coloration in males existed ($\chi^2=0.33$, df=1, $P>0.05$). Hence, males of island populations were not more likely to lose bright coloration than males in other geographic situations.

Species including both resident and migratory populations showed predictable patterns of geographic variation in sexual dichromatism. For example, the northern, migratory populations of the Shiny Cowbird *Molothrus aeneus* are dimorphic, but the southern, resident populations have the sexes alike and females brightly coloured like the northern males; many other examples of this pattern exist (e.g. *Parula americana–P. pitiayumi*, *Dendroica pinus*, *D. graciae–D. adelaidae*, *D. discolor–D. vitellina*, *Icterus cucullatus*, *Agelaius phoeniceus*). The association between permanent residency and bright (male-like) female plumage is striking and consistent in each of these taxa. Moreau (1960) presented evidence for an association between levels of dichromatism and mating system—polygynous species having dull-plumaged females, and monogamous species often having bright-plumaged females.

Discussion

A wide variety of adaptive hypotheses has been used to account for particular examples of geographic variation in sexual dichromatism; others not proposed specifically regarding this phenomenon can be applied to it in an equally valid manner. These ideas include contrasting selection pressures for migratory vs. permanent resident populations (Hamilton 1961), parasite-mediated sexual selection (Hamilton & Zuk 1982), interspecific female mimicry (Røskaft *et al.* 1986), reduced need for species recognition characters in insular populations (Mayr 1942, 1963), reduced need for predator signalling (Baker & Parker 1979), and absence of nutritional elements necessary for bright coloration (Abbott *et al.* 1977). Each of these hypotheses yields a slightly different set of predictions regarding the phenomenon; more than one, of course, may be acting in such a heterogeneous assemblage of species as that treated herein. Several depend critically on the assumption that bright plumage is costly, and that it will be lost in the absence of selection pressures in its favour.

Rather than entering into an overly nebulous discussion of how particular examples might fit the predictions of particular hypotheses, I will take a different direction in the discussion of my results. The genetic basis for plumage dichromatism appears to be quite simple in birds. Experiments by Morgan (1919) on hen-feathered breeds of chickens *Gallus domesticus* indicate that dichromatism in that species is controlled by but two loci which act via hormonal influences. Furthermore, rare variant morphs in populations of several of the species listed in the Appendix may well represent the expression of alleles for characters affecting plumage dichromatism: e.g. *Columba iriditorques*, *Pyrocephalus rubinus*, *Trochocercus cyanomelas–T. nitens*, and *Terpsiphone viridis*. Hence, characters related to sexual dichromatism may often have a simple Mendelian basis, or at least a simple sex-linked Mendelian basis, and different alleles of these genes may often be found segregating in natural populations of birds.

This observation leads me to suggest a possible alternative explanation for many of the occurrences of geographic variation in sexual dichromatism. Genetic drift in small, isolated populations of birds could lead to the loss or fixation of alleles for bright or dull male or female plumages, and could account for many of the odd patterns of variation documented in the Appendix. Inclusion of ideas from models of interactions between genetic drift and Fisherian runaway sexual selection (e.g. Lande 1980, 1981) could explain elevated evolutionary rates and the apparent concentration of examples in polygynous and lekking species. This alternative hypothesis has the advantages of not invoking novel selection pressures, of explaining all directionalities of change in particular geographic situations (e.g. *acquisition* of bright plumage in island populations), and of being able to explain the frequency of examples of this phenomenon in insular situations. Some hypotheses mentioned above may indeed prove to be the correct explanations for the evolution of particular examples of variation in sexual dichromatism; for example, the ideas of Hamilton (1961) and

Moreau (1960) appear to have explanatory power for migrant vs. resident populations of warblers. However, I suggest that the drift hypothesis may be applicable in more situations than the selective mechanisms.

Inspecting the few phylogenetic hypotheses available for groups included in the Appendix, it is clear that sexual dichromatism evolved dynamically in many lineages. For example, comparing sexual dichromatism characters with a recent hypothesis for the evolutionary history of the ducks (Livezey 1991) indicates several lineages in which dichromatic species arose from nondichromatic dull species, lineages in which dichromatism was lost, and indeed the full spectrum of possible changes. These conclusions are clearly preliminary, but the pattern of dynamic evolution of sexual dichromatism is clear. Further explorations of these ideas can be based on this and other phylogenetic hypotheses now available in the scientific literature.

Evolutionary changes in secondary sexual characters such as plumage coloration also may be important in the speciation process. This dimension of the phenomenon of geographic variation in sexual dichromatism is underemphasised in this paper because I limited the list in the Appendix to examples at the superspecies level or lower, that is, before the speciation process is completed by the establishment of sympatry. Populations under sexual selection that gain or lose patches of bright plumage may become reproductively isolated from one another rapidly, thus accelerating the process of formation of biological species in a manner more or less analogous to the mechanisms proposed by Kaneshiro (1980, 1983). Clear examples of secondary contact of D/D populations with B/D source populations include the rock-buntings *Emberiza tahapisi* and *E. socotrana*, and the pardalotes *Pardalotus punctatus* and *P. quadragintus*.

A final comment refers to the likelihood that Mayr's (1942, 1963) species recognition hypothesis would explain a significant number of the occurrences of geographic variation in sexual dichromatism. Many problems and inconsistencies plague it: (1) it can explain neither the *acquisition* of bright, species-specific female plumages in many insular bird species, nor (2) the occurrence of these phenomena in many continental species as well; (3) it invokes the idea of high costs of bright plumage as a reason for its loss in insular populations; (4) it requires that sexual selection for bright and gaudy male plumages not exist, so that relaxed selection for species-recognition characters can lead to loss of bright plumages; and (5) it requires the tenuous assumption that birds need bright and obvious plumage patches to be able to recognize and identify conspecifics. Hence, this hypothesis is unlikely to explain generally the occurrence of geographic variation in sexual dichromatism in birds.

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APPENDIX

Summary of examples of geographic variation in sexual dichromatism in birds. Parentheses () indicate populations polymorphic for a particular plumage combination. An asterisk * indicates the probable ancestral condition based on outgroup comparisons, where known; numbers indicate minimum numbers of independent derivations of particular plumage combinations; a plus sign + indicates an unknown number greater than one. Ellipses . . . after a species name indicate superspecies; for coloration, B=bright, D=dull, P=parapatric; for geographic situation, I=insular, C=continuous and clinal, and A=allopatric on continent.

Taxon	D/D	D+/D	B/D	B/D+	B/B	Geogr.	Ref.
ANATIDAE							
Chloephaga picta[1]	.	(+)	1	.	.	IC	Delacour 1950
Plectropterus gambensis[2]	.	1	1	.	.	P	Snow 1978
Anas americana . . .	.	.	+	1	.	A	—
A. strepera	.	1	*	.	.	I	Delacour 1954–1964
A. castanea–A. gibberifrons	+	.	+	.	.	AI	Ripley 1942
A. platyrhynchos	7	1	*	.	.	API	Delacour 1954–1964
A. acuta	2	.	*	.	.	I	Delacour 1954–1964
A. clypeata	.	+	*	.	.	A	Snow 1978
ACCIPITRIDAE							
Aviceda subcristata	.	.	1	*	.	I	Mayr 1945
Circus aeruginosus . . .[3]	1	*	1	.	.	AI	Cheke 1987b, Snow 1978
FALCONIDAE							
Falco tinnunculus	.	2	3	1	.	I	Cade 1982
MEGAPODIIDAE							
Megapodius freycinet[4]	*	2	.	.	.	I	Mayr 1938
CRACIDAE							
Crax pauxi-uniformis[5]	(1)	.	*	.	.	A?	Delacour & Amadon 1973
C. rubra . . .[6]	+	+(+)	+	.	+	P	Delacour & Amadon 1973
C. fasciolata	+	.	+	.	.	C	Delacour & Amadon 1973

Continued

APPENDIX continued

Taxon	D/D	D+/D	B/D	B/D+	B/B	Geogr.	Ref.
PHASIANIDAE							
Francolinus francolinus . . .	.	.	.	+	+	P	Hall 1963
F. erckelii . . .	.	.	.	2	*	A	Hall 1963
F. bicalcaratus . . .	.	.	.	1	*	P	Hall 1963
Synoicus ypsilophorus[7]	.	+	+	.	.	C	Mayr & Gilliard 1951, Mayr 1935
COLUMBIDAE							
Columba vitiensis	.	+	+	.	.	I	Goodwin 1983, Amadon 1943
C. delegorguei	.	+	+	.	.	C	Goodwin 1983
C. iriditorques–C. malherbii[8]	.	1	*	.	.	I	Amadon 1953
Aplopelia larvata	.	(+)1	1	.	.	CI	Goodwin 1983, Amadon 1943
Gallicolumba stairi–G. beccarii	.	.	+	+	+(+)	I	Goodwin 1983, Amadon 1943
Ptilinopus monachus . . .	.	.	1	.	*	I	Ripley & Birckhead 1942
P. perousii . . .	*	.	1	.	.	I	Ripley & Birckhead 1942
CUCULIDAE							
Chalcites lucidus	.	*	1	.	.	I	Mayr 1932b
Eudynamis scolopacea	+	.	*	.	+	I	Mayr 1944
APODIDAE							
Cypseloides rutilus–C. phelpsi	.	.	.	1	1	A	Meyer de Schauensee & Phelps 1978
TROCHILIDAE							
Florisuga spp.–*Melanotrochilus* spp.	.	.	1	.	1	A	Zimmer 1950
Heliodoxa schreibersii	.	.	.	1	1	P	—
H. branickii–H. gularis[9]	.	.	1	1	.	P?	—
Heliangelus amethysticollis	.	.	+	1	.	P?	—
H. exortis[10]	.	.	.	+(+)	+(+)	C	Bleiweiss 1985a,b
Schistes geoffroyi	.	.	1	1	.	P	—
Heliothryx barroti–H. aurita	.	.	1	1	.	P-A?	—

Continued

APPENDIX continued

Taxon	D/D	D+/D	B/D	B/D+	B/B	Geogr.	Ref.
TROGONIDAE							
Pharomachrus spp.	.	+	1	.	.	P-A?	—
ALCEDINIDAE							
Halcyon cinnamomina	+	+	.	.	.	I	Pratt *et al.* 1987
PHOENICULIDAE							
Phoeniculus castaneiceps	+	.	+	.	.	A	Snow 1978
GALBULIDAE							
Galbula albirostris–G. cyanicollis	1	1	.	.	.	P	—
CAPITONIDAE							
Eubucco versicolor . . .	.	.	+	+	.	P	—
Trachyphonus margaritatus . . .	.	.	1	1	.	P	Snow 1978
RAMPHASTIDAE							
Selenidera spp.	.	.	+	.	1	A	—
PICIDAE							
Sphyrapicus varius . . .	.	+	+	.	.	P	Howell 1952
Piculus rivolii	.	1	*	1	.	P-C	—
P. viridis	.	1	*	.	.	A?	Short 1982
FORMICARIIDAE							
Thamnophilus nigrocinereus	.	.	+	+	.	P	—
Sakesphorus canadensis . . .	1	1	+	1	.	P	—
Thamnomanes caesius–T. schistogynus	.	.	1	1	.	P	—
Myrmotherula haematonota . . .	.	1	*	.	.	A	—
Microrhopias quixensis	.	.	+	+	.	P	—
Pyriglena leuconota	.	.	+	+	.	P	Hellmayr 1929
Formicarius colma	.	.	*	.	1	P	—

Continued

APPENDIX continued

Taxon	D/D	D+/D	B/D	B/D+	B/B	Geogr.	Ref.
COTINGIDAE							
Rupicola rupicola–R. peruviana	.	.	1	1	.	A	—
PIPRIDAE							
Pipra coronata	.	+	+	.	.	P	—
Chloropipo unicolor	+	.	1	.	.	P-S	—
TYRANNIDAE							
Pyrocephalus rubinus[11]	(1)	(1)	*	.	.	I,P	Lack 1947
Myiopagis caniceps	(1)	.	1	.	.	A-P	—
ALAUDIDAE							
Eremopteryx verticalis	1	2	+	+	.	A-P	Hall & Moreau 1970
E. leucotis	.	.	.	1	1	P	Hall & Moreau 1970
HIRUNDINIDAE							
Progne modesta	1(1)	.	1	.	.	API	—
CAMPEPHAGIDAE							
Coracina caledonica	.	+	+	.	.	I	Mayr 1955
C. striata	.	+	*	+	.	I	duPont 1971
C. lineata	+	.	+	.	.	I	Mayr 1931
C. tenuirostris	.	.	+	+	.	I	Mayr 1955
Lalage sueurii[12]	1	.	*	.	.	A	Mayr 1940
L. aurea	+	*	+	+	.	I	Mayr 1941
L. leucopyga	(+)	.	*	.	.	I	Mayr 1941
IRENIDAE							
Aegithina tiphia–A. nigrolutea	+	+	+	.	.	PCI	Marien 1952

Continued

APPENDIX continued

Taxon	D/D	D+/D	B/D	B/D+	B/B	Geogr.	Ref.
LANIIDAE							
Dryoscopus cubla . . .	.	.	2	.	2	P	Hall & Moreau 1970
Tchagra cruenta[13]	.	.	.	+	+	PC	Hall & Moreau 1970
Laniarius ferrugineus . . .	.	.	*	1	.	PC	Hall & Moreau 1970
Telophorus multicolor . . .[14]	.	.	+	.	+	P	Moreau & Southern 1958, Hall *et al.* 1966
Lanius cristatus	.	.	.	+	+	AC	Hall & Moreau 1970
VANGIDAE							
Cyanolanius madagascarinus	.	1	*	.	.	I	Benson 1960
TURDINAE							
Saxicola torquata–S. borbonnensis	1	.	*	.	.	I	Hall & Moreau 1970, Cheke 1987 a,b
Oenanthe xanthoprymna . . .	.	.	+	(+)	.	AP	Hall & Moreau 1970, Vaurie 1949
O. lugens	.	+	+(+)	.	.	AP	Hall & Moreau 1970, Vaurie 1949
O. monticola . . .	.	.	1	1	1	AP	Hall & Moreau 1970
Myrmecocichla arnotti	.	.	+	.	1	AP	Hall & Moreau 1970
Thamnolaea cinnamomeiventris	.	.	*	1	.	A	Hall & Moreau 1970
Monticola saxatilis . . .	.	1	*	+	.	AP	Hall & Moreau 1970
ORTHONYCHINAE							
Eupetes castanonotus	.	.	*	1	.	AP	Rand 1940b
POLIOPTILINAE							
Polioptila plumbea	.	.	.	+	+	P	—
SYLVIINAE							
Apalis flavida	*	+	.	.	.	P	Hall & Moreau 1970
A. jacksoni–A. chariessa	.	1	1	.	.	A	Hall & Moreau 1970
A. rufogularis–A. argentea	.	.	+	.	+	P	Hall & Moreau 1970
A. sharpii–A. porphyrolaema	+	1	.	.	.	A	Hall & Moreau 1970
Bathmocercus cerviniventris . . .	.	1	1	1	.	A	Hall & Moreau 1970
Hyliota flavigaster . . .	.	.	1	1	1	P	Hall & Moreau 1970

Continued

APPENDIX continued

Taxon	D/D	D+/D	B/D	B/D+	B/B	Geogr.	Ref.
MALURINAE							
Malurus lamberti	.	.	1	1	.	PC	Schodde 1982
M. alboscapulatus	.	.	*	2	3	AP	Schodde 1982
MUSCICAPINAE							
Ficedula hypoleuca	+	+	+	.	.	C	Røskaft *et al.* 1986
Niltava poliogenys[15]	1	1	.	.	.	P?	—
Petroica multicolor	3	.	*	.	2	I	Mayr 1934, 1942
P. cucullata–P. vittata	1	.	*	.	.	I	Keast 1961
PLATYSTEIRINAE							
Batis capensis . . .	.	1	2	1	1	AP	Hall & Moreau 1970
B. molitor–B. minima	.	.	*	1	.	P	Hall & Moreau 1970
Platysteira cyanea . . .	.	.	1	2	1	P	Hall & Moreau 1970
MONARCHINAE							
Trochocercus cyanomelas–T. nitens[16]	.	1	1	.	.	P	Hall & Moreau 1970
Terpsiphone viridis[17]	.	+	+	.	.	P	Chapin 1948
T. rufocinerea	1	1	1	.	.	P	Chapin 1948
T. mutata–T. bourbonnensis	(+)	.	*	.	.	I	Cheke 1987a,b
T. rufiventer[18]	2	2	2	.	.	PI	Chapin 1948
Chasiempis sandwichensis	.	.	.	+	+	AP	Pratt 1980
Pomarea spp.[19]	.	+	+	+	+	I	Murphy 1938
Clytorhynchus vitiensis–C. nigrogularis	1	.	1	.	.	I	Pratt *et al.* 1987
Monarcha castaneiventris . . .	.	.	.	1	+	I	Mayr 1945
PACHYCEPHALINAE							
Pachycephala pectoralis . . .	2	2+	*	2+	1	I	Galbraith 1956
DAPHOENOSITTINAE							
Neositta papuensis[20]	.	+	+	.	.	A?	Rand 1940a

Continued

APPENDIX continued

Taxon	D/D	D+/D	B/D	B/D+	B/B	Geogr.	Ref.
DICAEIDAE							
Melanocharis spp.	2	.	*	.	.	P	Salomonsen 1960a, Mayr & Amadon 1947
Dicaeum hypoleucum	*	1	.	.	.	P	Salomonsen 1960b
D. aeneum–D. tristrami	1	.	*	.	.	I	Salomonsen 1960b
NECTARINIIDAE							
Anthreptes collaris	.	.	1	1	.	P	Hall & Moreau 1970
A. rectirostris	.	1	1	.	.	AP	Hall & Moreau 1970
A. longuemarei . . .	1	.	+	+	.	P	Hall & Moreau 1970
Nectarinia bifasciata	.	(1)	1	.	.	P	Hall & Moreau 1970
N. olivacea	+	+	+	.	.	PC	Hall & Moreau 1970
N. verticalis	.	.	+	+	.	P	Hall & Moreau 1970
N. reichenbachii	.	.	+	.	*	I	Hall & Moreau 1970
MELIPHAGIDAE							
Myzomela cardinalis	.	1	1	.	.	I	Mayr 1932a
M. nigrita	+	+	.	.	.	I	Mayr 1932a
EMBERIZINAE							
Sicalis olivascens	.	.	+	+	.	P	Meyer de Schauensee 1970
Sporophila bouvreuil	.	1	+	.	.	P	—
Loxigilla violacea–L. portoricensis	.	.	*	1	.	I	Bateson 1913
L. noctis	1	.	*	.	.	I	Bond 1980
Certhidea olivacea	*	.	(1)	.	.	I	Grant 1986
Pipilo erythrophthalmus	.	.	+	+	+	C	—
Arremon taciturnus	.	.	+	+	+	P	—
THRAUPINAE							
Creurgops verticalis–C. dentata	1	1	.	.	.	A	Meyer de Schauensee 1970
Habia spp.	.	.	*	1	.	P	—
Spindalis zena	.	.	*	+	.	I	—
Euphonia musica	.	1	*	.	.	I	Bateson 1913

Continued

APPENDIX continued

Taxon	D/D	D+/D	B/D	B/D+	B/B	Geogr.	Ref.
PARULIDAE							
Parula americana–P. pitiayumi	.	.	.	1	1	A	—
Dendroica pinus	.	.	.	1	1	C	—
D. graciae–D. adelaidae	.	.	.	+	1	IC	—
D. discolor–D. vitellina	.	.	.	1	1	I	—
DREPANIDIDAE							
Loxops maculata	2	3	1	.	.	I	Amadon 1950
L. coccinea	.	1	*	.	.	I	Amadon 1950
ICTERIDAE							
Icterus cucullatus	.	.	+	1	.	AP	Hamilton 1961
Quiscalus niger–Q. lugubris	.	.	+	+	+	I	—
Agelaius phoeniceus	.	.	+	1	.	I	—
A. cyanopus	.	.	+	1(1)	.	A	—
Molothrus aeneus	.	.	+	+	+	C	—
CARDUELINAE							
Serinus citrinelloides	.	+	+	+	.	AP	Hall & Moreau 1970
S. donaldsoni	.	.	1	1	.	P	Hall & Moreau 1970
Acanthis cannabina	1	*	1	.	.	A	Hall & Moreau 1970
Loxia curvirostra	+	+	+	.	.	C	Griscom 1937
Pyrrhula pyrrhula	2	.	*	.	.	I,P	Vaurie 1956
ESTRILDIDAE							
Uraeginthus angolensis	.	.	.	+	+	P	Goodwin 1982
Estrilda melanotis	1	.	2	.	.	A	Goodwin 1982
PLOCEIDAE							
Ploceus xanthops–P. subaureus[21]	.	.	1	.	1	P	Hall & Moreau 1970
P. baglafecht . . .	1	1	.	.	.	P	Hall & Moreau 1970, Moreau 1960
Malimbus scutatus–M. cassini	.	.	1	1	.	P	Hall & Moreau 1970
M. erythrogaster–M. ibadanensis[22]	.	1	*	.	.	A	Hall & Moreau 1970
Foudia rubra	2	.	*	.	.	I	Cheke 1987a

Continued

APPENDIX continued

Taxon	D/D	D+/D	B/D	B/D+	B/B	Geogr.	Ref.
STURNIDAE							
Cinnyricinclus leucogaster	.	.	*	.	+	P	Hall & Moreau 1970
CRACTICIDAE							
Gymnorhina tibicen	.	+	+	+	.	P	Amadon 1951
PTILONORHYNCHIDAE							
Amblyornis spp.	1	.	*	.	.	A	Cooper & Forshaw 1977, Gilliard 1969, Mayr & Jennings 1952
Chlamydera spp.	2	.	1	1	+	AIC	Cooper & Forshaw 1977, Gilliard 1969, Mayr & Jennings 1952

1. Insular form is B/D; mainland form in polymorphic B/D (D+/D). **2.** Different characters make up the "male" character in the two populations. **3.** Insular population is more dimorphic than those of mainland; allopatric population is D/D. **4.** One of the D+/D populations is apparently a hybrid population between two differentiated D/D populations; each sex of the hybrid population apparently resembling a different parental population. **5.** Evidence indicates a decline of the dull-female morph over the past 100 years, espccially in regions where hunting pressure is strong. **6.** Thrce characters vary apparently independently, with extremely complex geographic patterns. **7.** Less dimorphic forms occur at higher elevations and at higher latitudes. **8.** Populations of *C. iriditorques* on the coast adjacent to island show a rare dull-male morph like the plumage of *C. malherbii*. **9.** Females appear to be variable in resemblance to males. **10.** Some populations have polymorphic bright and dull females; others have continuous variation in brightness of females. **11.** Individuals of both sexes of the coastal Peruvian race *obscurus* occasionally show a uniform grey plumage. **12.** Males in one set of populations have a dull, off-season plumage present neither in other populations of the species, nor in other species of *Lalage*. **13.** Sexes reversed, actually D+/B→B/B. **14.** Dauntingly complex variation among sexes, across geography, and among individuals makes interpretation difficult. **15.** Two plumage characters vary independently, one clinally D/D→B/D+, the other discretely (non-clinally) B/D→B/B. **16.** This species is a D/D member of an otherwise B/D genus. **17.** FMNH 197744, apparently a female, has an iridescent throat like male, though this species is normally dull-female. **18.** Males vcry polymorphic; extremely complex patterns of variation. **19.** Very complex and striking variation; sexes appear to vary independently. **20.** Some populations appear to have the female brighter than male in the geographically variable character. **21.** Female dull in nonbreeding plumage only in B/D population. **22.** Both sexes show combination of bright colours—*M. ibadanensis* less dichromatic, but difficult to decide which sex is brighter.